

THE HYMENOPTEROUS POISON APPARATUS:
EVOLUTIONARY TRENDS IN THREE CLOSELY RELATED
SUBFAMILIES OF ANTS (HYMENOPTERA: FORMICIDAE)

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ABSTRACT

Although there is a general similarity in the basic structure of the poison apparatus in hymenopterous insects, there are individual characteristics that may be significant to an understanding of phylogenetic relationships between and within the various groups. In all members of the subfamily Ponerinae investigated, with the exception of one species, a sclerite known as the furcula is present. The form of this sclerite varies considerably among species of this subfamily and most stinging members of other subfamilies. The furcula is lacking in members of the Dorylinae, 4 members of the Cerapachyinae and one member of the Ponerinae examined. An explanation of the significance of this and other sclerites, as well as comments on the soft parts of the poison apparatus are presented. An examination of the sting sclerites of Old and New World Dorylinae indicates that there is some morphological distinction between certain groups within that subfamily.

Key Words: Poison apparatus, Formicidae, ants, evolution of ants, morphology, phylogeny.

INTRODUCTION

The phylogenetic placement of subfamilies in the family Formicidae has received much attention in the past (Brown 1954; Eisner and Brown 1958; Wilson, Carpenter and Brown 1967a, 1967b). Ants, according to the presently accepted phylogenetic scheme, presumably arose from a tiphioid ancestor through two lines of evolution (Myrmecioid and Poneroid Complexes). Further evidence has shed some light on an understanding of the relationship between myrmecioid ants and wasps through the discovery of *Sphecomyrma freyi* Wilson, Carpenter and Brown, the most primitive formicid known to science.

Within the Poneroid Complex, little information has been presented in support of any close relationships between the subsequent subfamily groups. Some evidence has been provided in support of the theory that the Ponerinae and Dorylinae may have had a common ancestor (Wilson 1958; Hermann and Blum 1967b; Hermann 1968c). In the past, members of the Cerapachyinae have been considered to be closely related to the Ponerinae (Brown and Nutting 1950; Brown 1954). Robertson (1968) presented some interesting findings concerning these and some other ant subfamilies in her work on Australian Hymenoptera. The present investigation was initiated as part of a comparative study of the hymenopterous poison apparatus in some members of the Ponerinae, Dorylinae and Cerapachyinae.

MATERIALS AND METHODS

Whenever possible, live material was used. However, many specimens were taken from preserved laboratory collections while the more uncommon species were procured from dry, pinned material. Specimens were dissected and treated in the manner outlined by Hermann and Blum (1966). All measurements for illustrations are in millimeters.

RESULTS

The importance of using live specimens, especially when freshly collected in the field, cannot be overemphasized. It is extremely difficult, and often impossible, to investigate the soft parts of the poison apparatus, particularly the free filaments, from preserved material. This is, no doubt, what caused some investigators to conclude that the free filaments in certain ant species are absent during some periods of adult existence. Because fresh specimens were not always available for examination in this investigation, the soft parts of many species have not been included in illustrations.

In the study of muscle attachments, dried specimens are often superior to freshly collected or preserved material. This is due to the brown coloration that many muscles assume when they become dried. The brown appearance in whole mounts facilitates observations on muscle origin and insertion that may otherwise be extremely difficult.

Soft Parts of the Poison Apparatus

Due to the unavailability of live members of the Cerapachyinae, information concerning the soft parts of their poison apparatus is lacking in this investigation.

Poison Sac (= Acid Gland = Venom Reservoir, PS, Fig. 1, A—E).—In general, the poison sac in ponerines and dorylines is elongate and often pear-shaped in appearance. As has been pointed out in previous articles, this sac functions as a reservoir for venom until it is employed during the act of stinging.

Convolute Gland (CG, Fig. 1, A—C, E).—The convolute gland in members of the Ponerinae and Dorylinae has been discussed by Hermann and Blum (1966, 1967b). This gland in all ants, other than the Formicinae (Hermann and Blum 1968), seems to be located within the poison sac and is composed of polygonal cells that border small ductules. The ductules empty into larger ducts that in turn empty into the poison sac. The convolute gland attaches to a duct (CD) that passes basad in the sac, exits as a single duct from the sac and finally branches into two filamentous structures known as the free filaments (FF).

Dufour's Gland (= Alkaline Gland, DG, Fig. 1, A, B, D).—Dufour's gland in the Ponerinae and Dorylinae is generally an elongate sac of cuboidal or columnar cells. Except in some myrmecine species, the function of this gland is not well known. In species of the genera *Solenopsis* Westwood and *Pheidole* Westwood, Dufour's gland has been shown to be the source of a trail following pheromone. No function has been attributed to the products of this gland in any other formicid genera.

Free Filaments (FF, Fig. 1, A—C, E, F).—The free filaments branch from a common duct (CD) that extends from the base of the poison sac in the ponerines and dorylines examined. Although earlier studies of *Rhytidoponera metallica* F. Smith and *Stigmatomuna pallipes* (Haldeman) indicated that the filaments extended from the sac apex (Whelden 1958a, 1958b), I have found that the filaments of these and other members of the Ponerinae extend from the base of the sac. This was also the case in dissections reported by Robertson (1968) on members of the Ponerinae.

The filaments usually maintain a relatively uniform diameter throughout their length in both subfamilies. However, the possession of uniform filaments is not a distinct character of all ponerine ants, as was shown for *Leptogenys elongata* (Buckley) by Hermann (1969). The filaments possess

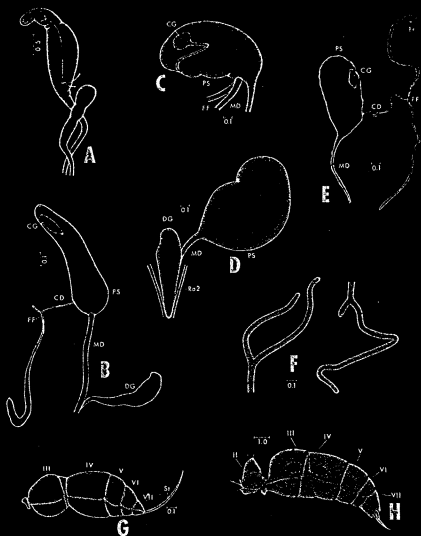


Fig. 1.—Some soft parts of poison apparatus and lateral views of gasters. A — Poison sac and Dufour's gland of *Leptogenys elongata* (Buckley) (LV). C — Poison sac of *Neivamyrmex nigrescens* (Cresson) (LV). D — Poison sac and Dufour's gland of *Neivamyrmex nigrescens* (VV). E — Poison sac of *Rhytidoponera metallica* F. Smith (LV). F — Branching of the free filaments in *Neivamyrmex nigrescens*. G — Gaster of *Onychomyrmex hedleyi* Emery (LV), illustrating extended sting from posterior region of gaster. H — Gaster of *Termitopone commutata* Roger (LV), illustrating exsertile sting.

a central lumen that is lined by simple cuboidal to columnar epithelium. Branching of the filaments has been found in most hymenopterous species, including members of the Ponerinae and Dorylinae.

Skeletal Components

The gonapophyses that make up the sting in species of the Ponerinae and Cerapachyinae are usually exsertile (protruding from the posterior region of the gaster) (Fig. 1, G, H) while the stings of doryline species are often insertile (positioned fully within the gaster). An exsertile or extrusible sting is usually a character shared by primitive formicids such as members of the Myrmecilinae and Ponerinae. Such is the case also in *Aneuretus simoni* Emery (Hermann 1968b). The insertile condition in dorylines is well illustrated in Old World species. Sclerites that make up the poison apparatus have arisen from the 8th, 9th and 10th abdominal segments and their gonapophyses. All of the sclerotized parts of the poison apparatus are paired structures except the sting, furcula, anal arc, anal pad and sometimes the spiracular plates.

First Valvifers (= First Gonocoxae = Triangular Plates, TP, Figs. 2, 3, 7, 8). — The shape of the first valvifers varies considerably throughout the Hymenoptera, although they are easily recognizable as triangular plates in all specimens whether the poison apparatus is well developed (as in all stinging forms) or extremely reduced (as in the Dolichoderinae and Formicilinae). Each of these structures, synonymous with the gonangulum of Scudder (1961), is an important sclerite in stinging Hymenoptera since it is responsible for alternating movements of the lancets. In general, there has been some modification of the triangular plates throughout the Hymenoptera, which has resulted in a diverse array of structures illustrated in the accompanying figures. The triangular plate in *Dorylus* (*Anomma*) *molestus* (Gerstaecker) (Fig. 3, E) has undergone reduction. These structures are usually elongate in some of the Dorylinae and reduced considerably in the Dolichoderinae and Formicilinae. Although diversification is well demonstrated in the triangular plates of various hymenopterans, the area of most sclerotization is in the regions of articulation with the quadrate and oblong plates.

The first and second rami (Ra 1 and Ra 2), representing the basal regions of the first and second gonapods, are very long and considerably flexible and their shape depends on the position of associated sclerites (i.e., whether certain muscles are contracted or extended). The flexibility of the rami and varying degree of contraction of the muscles in preserved specimens results in the sclerites being found in a number of positions when the ants are dissected.

In all respects, the triangular plates have maintained the same relative relationships with other sclerites in all of the species examined in this and previous investigations. Their close relationship with the oblong plates is illustrated for *Eciton hamatum* (Fabricius) (Fig. 7, B).

First Valvulae (= First Gonapophyses = Lancets, Ln, Fig. 3, E). — Lancets were present in all of the hymenopterous insects examined, although they were reduced in some of the Dorylinae. Reduction of the lancets involves loss of the valve (Va), a structure that functions during venom release. Loss of the value has occurred in *Dorylus* (*Anomma*) *molestus* and some myrmecines (e.g., *Atta texana* (Buckley) and *Atta cephalotes* (L.)). All stinging species examined possessed this sclerite.

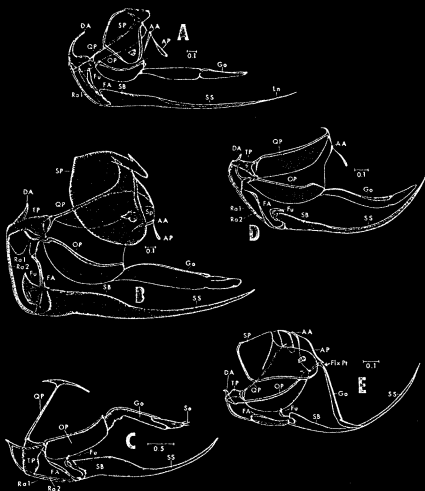


Fig. 2. — Poison sclerites of some Ponerinae (LV). A — *Leptogenys elongata*. B — *Neoponera villosa* (Fabricius). C — *Termitopone commutata*. D — *Amblyopone australis* Erichson. E — *Onychomyrmex hedleyi*.

Usually, the distal tip of the lancets in stinging Hymenoptera possesses several barbs that generally function in cutting the wound in order to insert the sting. These barbs are generally present in the Ponerinae but not in the Dorylinae. The distal tip of the lancet of *Dorylus* (*Anomma*) *molestus* is membranous.

Second Valvifers (= Second Gonocoxae = Oblong Plates, OP, Figs. 2, 3, 7, 8). — Oblong plates seem to be present in all hymenopterous insects, although their rami and valvulae may be reduced or absent in the Dolichoderinae and Formicinae. They are always elongate, slender structures. Near the point of articulation with the triangular plate there are a number of setae that presumably serve a sensory function when the two sclerites articulate with one another.

Muscles 3 (deflecting muscle of the sting) and 4 (rotating or pivoting muscle of the sting) originate on the oblong plate and insert on the furcula in most members of the Ponerinae. In the Dorylinae, Cerapachyinae and *Simopelta oculata* Gotwald and Brown of the Ponerinae in this investigation, these muscles insert on the anterior extension (New World Dorylinae and *Simopelta*) or merely the anterior region of the sting bulb (Old World Dorylinae and Cerapachyinae).

Second Valvulae (= Fused Second Gonapophyses = Sting. St, Figs. 2-8). — The sting consists of a proximal sting bulb (SB) and distal sting shaft (SS). It is usually an extremely slender structure but in some of the Old World dorylines (Fig. 8, G-I) the sting takes on a broad spatulate appearance. A number of nonstinging myrmecines possess a sting of this latter type.

The anterior region of the sting in most ponerines articulates with the two ventral apodemes of a furcula (Fu). This latter structure functions in deflection and rotation or pivoting of the sting (Hermann and Blum 1967b, Hermann 1968c) and therefore serves an important role during the stinging act. All members of the Dorylinae (Fig. 3, C, H; Figs. 4-7; Fig. 8, D, G—J) and Cerapachyinae (Fig. 8, A—C, F) and *Simopelta oculata* (Fig. 3, D) in this investigation lack a furcula.

The shape and size of the sting varies considerably among hymenopterous species. An extremely well developed and specialized sting is found in the Mutillidae (Hermann 1968a) whereas it has been lost in the Formicinae (Hermann and Blum 1968). Generally, ponerines, some dorylines and cerapachyines of the Formicidae possess a relatively large sting, whereas some members of the two latter groups possess relatively small ones. Within the Dorylinae there is some distinction between the stings of the genera *Aenictus*, *Dorylus*, *Labidus* and the other groups investigated. The stings of species of *Eciton*, *Neivamyrmex*, *Cheliomyrmex* and *Nomamyrmex* all possess a well developed anterior extension of the sting bulb (Figs. 3, H; 4, A, C, F, G; 5; 6; 7; 8, D). The anterior end of the sting bulb in *Labidus* appears to be somewhat truncate (Fig. 4, B, E). The sting of *Dorylus* (*Typhlopone*) sp. (Fig. 8, G), *Dorylus* (*Dorylus*) *braunsi* Emery (H) and *Dorylus* (*Anomma*) *molestus* (I) all are broad in appearance except distally. These three subgenera of *Dorylus* possess anterolateral extensions of the sting bulb rather than a single anterior extension. Muscles 3 and 4, nevertheless, attach to the anterior region of the sting bulb. *Aenictus gracilis* (F. Smith) has a sting that is relatively thinner than the sting found in *Dorylus* (H) (Fig. 8, J). The sting of *A. gracilis* has anterolateral exten-

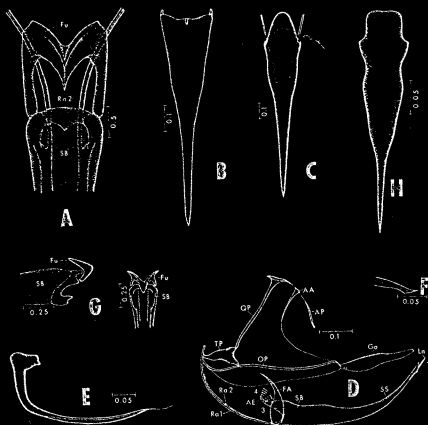


Fig. 3. — Poison sclerites of some Ponerinae, Dorylinae and Cerapachyinae. A — Furcula and anterior region of sting bulb of *Neoponera villosa* (DV). B — Sting of *Splinctomyrmex steinheili* Forel (DV), illustrating lack of furcula. C — Sting of *Eciton dulcius crassinode* Borgmeier (DV). D — *Sinopleta oculata* (LV), illustrating anterior sting bulb extension and insertion of muscles 3 and 4. E — Lancet of *Dorylus* (*Anomma*) *molestus* (Gerstaecker) (LV). F — Distal tip of sting of *Termitopone commutata* Roger (L & DV). G — Furcula and interior region of sting bulb of *Sinopleta oculata* (LV). H — Sting of *Neivamyrmex postcarinatus* Borgmeier (DV).

sions and muscles 3 and 4 insert on the anterior region of the sting bulb.

The distal tip of the sting is generally a simple pointed structure. However, in *Simopelta oculata*, the tip expands distally after a gradual posterior taper (Hermann 1968c).

Third Valvulae (= Gonostyli, Go, Figs. 2, 3, 7, 8). — In many species of the Hymenoptera, each gonostylus is separated into distal and proximal sclerites by a narrow nonsclerotized region and usually by a peripheral constriction. The distinction between proximal and distal portions is well illustrated in the Ponerinae in this investigation (Fig. 2), but not in the Cerapachyinae and Dorylinae (Fig. 7, C, D; Fig. 8, D, J). The significance of proximal and distal gonostylar sclerites seems evident in some insects with modified stings (Hermann 1968a) but not in most hymenopterous species.

Fuleral Arms (FA, Figs. 2, 3, 7, 8). — The bases of the fuleral arms are usually broad and well sclerotized, and the distal tip usually tapers to a point. At their basal point of articulation with the sting, they act as points of pivot for the deflection and rotation (Ponerinae except *Simopelta*) and pivoting (Dorylinae, Cerapachyinae and *Simopelta* in the Ponerinae) of the sting upon contraction of muscles 3 and 4. These arms also act as points of origin for muscles that close the poison canal within the sting (Hermann and Blum 1966).

Quadrate Plates (= 9th Hemitergites, QP, Figs. 2, 3, 7, 8). — These plates usually have a well sclerotized central bar with less sclerotized marginal wings. The dorsoposterior end (distal tip) forms a T-shaped apodeme that receives the protracting and retracting muscles of the lancets.

Spiracular Plates (= 8th Hemitergies, SP, Fig. 2, B, E; Fig. 8, D). — The spiracular plates are usually joined to each other by a dorsal bar. Whether a well sclerotized bar is present or absent, the 8th hemitergites always possess membranous connections with each other. The spiracular plates act as points of insertion for muscles that raise and lower the entire apparatus.

Anal Arc (= 10th Tergite, AA, Fig. 2, 3, 7, 8). — This structure, representing the tenth tergum, has been found in all ants and is associated ventrally with an anal pad (AP) that hangs ventrad toward the gonostyli and sting. The function of the anal pad is not known; these structures are often not well sclerotized and at times are difficult to examine in detail.

Furcula (Fu, Fig. 2, A — E; Fig. 3, A, G). — This structure has been found in many hymenopterous insects. In the Dorylinae, Cerapachyinae and in *Simopelta oculata*, it seems to have fused with the sting bulb in the course of evolution (Hermann 1968c). A furcula has been found in all ponerine species, except *Simopelta oculata*, and the form of this sclerite is quite diverse. Its two ventral apodemes articulate with the anterior region of the sting bulb and during contraction of muscle 3, the furcula is forced posteriad to move the anterior region of the sting posteriad and slightly dorsad. The sting pivots at the points of articulation with the fuleral arms, causing the distal tip of the sting to be deflected. In the Dorylinae and Cerapachyinae, muscle 3 functions in the same manner. In most members of the Ponerinae, muscle 4 contracts, causing the furcula to rotate from side to side and in turn causing the sting to rotate. In the Dorylinae, Cerapachyinae and *Simopelta* (Ponerinae) in this investigation, there is no furcula and muscle 4 inserts on the anterior region of the sting bulb. Con-

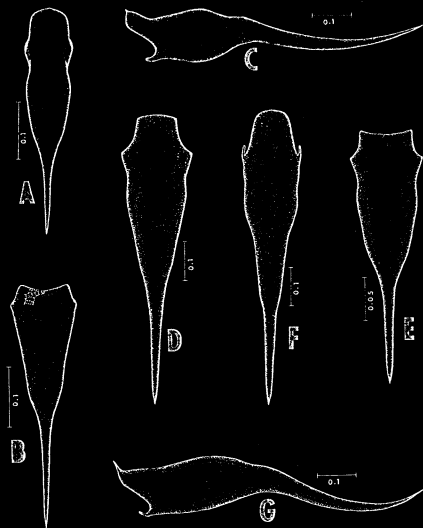


Fig. 4.—Stings of some New World Dorylinae. A—*Neivamyrmex wheeleri* (DV). B—*Labidus coecus* (Latreille) (DV). C and D—*Nomamyrmex hartigi* (Westwood) (L & DV). E—*Labidus spininodis* (DV). F & G—*Eciton lucanoides* (Emery) (D & LV).

traction of this muscle in these species results in a pivoting action by the sting. The points of articulation between sting and funicular arms which act as pivoting points for sting deflection, also act as pivoting points for lateral movement of the sting upon contraction of muscle 4.

DISCUSSION

The relationship between ponerines and dorylines has been discussed to some degree by Hermann and Blum (1967b) and Hermann (1968c, 1969). Obvious behavioral similarities between the two subfamilies (nomadism and group predation) have been reviewed by Wilson (1958). The ant species in these subfamilies, together with the Cerapachyinae, Myrmicinae and Leptanillinae, make up what Brown (1954) calls the Poneroid Complex. Although Robertson (1968) challenged Brown's scheme in her work on some of the major groups of the Hymenoptera, more work must be done before the phylogenetic pattern is clearly understood. Much of Robertson's hypothesis originated from work on the soft parts of the poison apparatus (i.e., glandular and reservoir regions), areas that do remain relatively stable in appearance in most ant subfamilies. I do not agree that the poison sac of species in the Formicinae is similar in any way with that of the Ponerinae except in the physiology and histology of the various regions and in that the free filaments extend from the base of the sac (Hermann and Blum 1968). Likewise, the sac of myrmecines is different from that of ponerines and members of the subfamily Myrmecinae. At this juncture, I have found only slight differences between the glandular and reservoir regions of the Ponerinae and Myrmecinae.

The filaments of ponerines, dorylines and myrmecines are generally extremely slender; they vary only slightly in diameter from the proximal to the distal regions and there is a common duct extending from the sac to the forked filaments. These characters are shared by members of the Formicinae. However, the convoluted gland in formicine species is not invaginated into the sac as it is in species of all other subfamilies. Species of the Pseudomyrmecinae possess a common duct as is found in the former subfamilies but the filaments do not maintain a uniform diameter throughout their length. Members of the Dolichoderinae possess globose filaments that lie adnate to the sac and have no common duct extending from the sac. Myrmecine ants possess filaments that branch at the surface of the sac, and thus lack a common duct, and the filament diameter increases from the proximal to the distal region. Although there is considerable variation among these structures throughout the Formicidae, the general plan of the venom producing and storing systems consisting of a sac, convoluted gland and filaments is quite similar in function in all ants (Blum and Hermann 1969).

The cerapachyines have long been considered closely related to the ponerines (Brown and Nutting 1950), and although several cerapachyine genera produce normal winged or ergatoid females, at least one genus (*Acanthostichus*) produces dichthadiiform females, a doryline character. Based on poison apparatus morphology in this investigation, the Cerapachyinae seem not to be as closely related to the Ponerinae as was once believed. Cerapachyines, at times, have been considered transitional stock between the Ponerinae and Dorylinae (Brown and Nutting 1950), suggesting that dorylines may have arisen from cerapachyinelike stock. How-

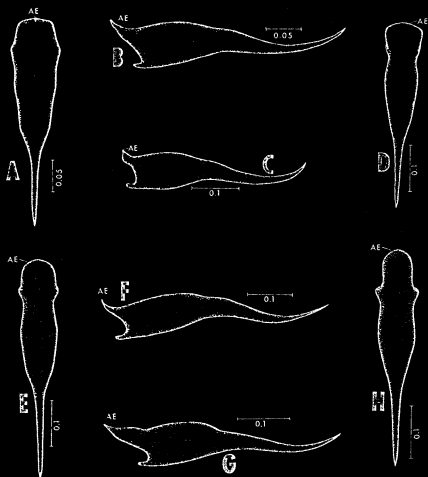


Fig. 5.—Stings of some species of the genus *Neivamyrmex*. A & B—*N. opacithorax* (Emery) (D & LV). C & D—*N. carolinensis* (L & DV). E & F—*N. pilosus* (F. Smith) (D & LV). G & H—*N. gibbatus* (Borgmeier) (L & DV).

ever, cerapachyines show vestigial legs and more advanced reduction in wing venation than the Dorylinae (Brown 1954).

In this study, it is apparent that there are some anatomical similarities between the poison apparatuses of the Cerapachyinae and Dorylinae. None of the species of either subfamily has a furcula and all possess the two muscle groups normally inserting on the furcula in most Ponerinae. Based on these data, then, cerapachyine stock (5, Fig. 9) should have parted from the ponerine line at about the same time as the dorylines or shortly afterward, indicating that dorylines may very well have arisen from cerapachyinelike stock or the two groups very likely could have a common ancestor.

Based on both morphological and behavioral data, there seems to be no doubt that cerapachyines, dorylines and ponerines are closely related. The question is how they are related to one another in an evolutionary scheme. Since not much is known about cerapachyine behavior, it is difficult to determine how they fit into this scheme behaviorally. Wilson (1958) outlined specific evolutionary steps probably taken by doryline groups in their acquisition of group-predatory and nomadic traits. It was assumed at that time that ponerines exhibiting these traits also probably followed the same evolutionary sequence as did the dorylines. A further implication arising from these data is that the Dorylinae may have arisen from a ponerinelike ancestor and consequently would have a direct connection with that subfamily. However, at that time this latter hypothesis needed more supporting evidence.

The presence of a furcula in most ponerines should certainly separate them by a considerable gap from the cerapachyines and dorylines, although this does not mean that these groups are not related. The fact that *Simopelta oculata* does not possess a furcula but does possess the muscles (3 & 4) that insert on the sting bulb seems to indicate that there may be some connection between the furculate and nonfurculate groups although this loss of a furcula may have arisen in later convergence. According to Gotwald and Brown (1966) and Hermann (1968c), *Simopelta oculata* is distinctly dorylinelike morphologically and behaviorally. It seems that *Simopelta* may indeed be considered an important genus in future work concerning the phylogeny of doryline and ponerine ants.

Intrasubfamily differences in the Dorylinae seem to indicate that there are 4 distinct types of stings present (Fig. 9). These are 1) the broad, spatulate sting of the Dorylini (10) with extensive anterolateral extensions of the sting bulb, 2) the relatively slender sting of the Aenictini (11) that possess less well-defined anterolateral extensions of the sting bulb, 3) the sting of Chelloniomyrmecini and most Ecitonini (12) with a well defined anterior sting bulb extension and 4) the anteriorly truncate sting of species of *Labidus* (13). Borgmeier (1955) considers *Labidus* to be the most primitive ecitonine. Based on previous anatomical evidence, *Neivamyrmex* and *Nomamyrmex* are considered closely related to *Labidus* and these genera are in turn related to *Eciton*. Laboratory tests by Watkins (1964, 1966, 1967) indicate that there is some intergeneric trail following between *Eciton*, *Neivamyrmex* and *Labidus*, indicating that, in part, there is some chemical similarity among these ecitonines. There is also some indication that similar myrmecophilous insects may be associated with *Nomamyrmex* and *Labidus* (Akre and Rettenmeyer 1966, Rettenmeyer 1963). Since only

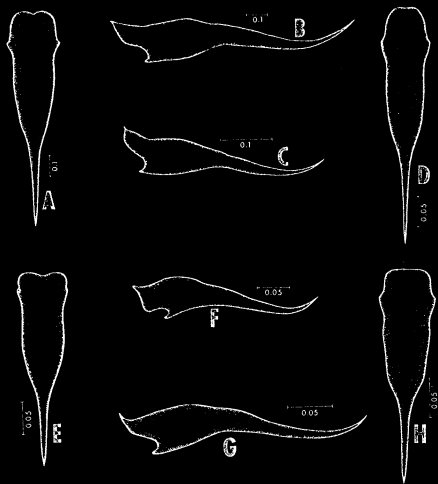


Fig. 6. — Stings of some species of the genus *Neivamyrmex*. A & B — *N. sumichrasti* (D & LV). C & D — *N. legionis* (L & DV). E & F — *N. agilis* (D & LV). G & H — *N. humilis* (Borgmeier) (L & DV).

one species of *Nomamyrmex* was examined in this investigation, a more thorough investigation of this genus and *Labidus* may reveal a closer connection between the two genera. However, at this time, the anterior end of the sting of the species here representing the two genera is different. However, the general diameter versus length of the entire sting in all New World dorylines seems to be much the same.

Based on poison apparatus morphology, I believe that there can be no mistake in the difference between Old and New World dorylines. Only members of the Dorylini and Aenictini in this investigation possess a concave anterior border of the sting bulb and anterolateral extensions. Although these two features are common characters between these two tribes, their stings are considerably different from each other. The sting of *Aenictus* in no other way, except in general composition, resembles that of *Dorylus*.

In conclusion, the theoretical evolution of the Ponerinae and certain members of the Dorylinae and Cerapachyinae, based on sting anatomy and some behavioral information, may be best represented by a cladogram as illustrated in Fig. 9. A separation arose between the Ponerinae and Dorylinae at the time of or before fusion between the furcula and sting bulb occurred (4 and 7). Fusion between these two areas in *Simopelta oculata* (6) probably occurred a little later than the separation between the two subfamilies. Separation between cerapachyines (5) and dorylines presumably occurred later. The next large evident break is in the Dorylinae, between New and Old World groups (8 and 9). In most New World dorylines (8), the sting bulb possesses a definite anterior extension whereas the old world species lack this character but possess anterolateral extensions of the sting bulb (9). A later separation occurred between the tribes Dorylini (10) and Aenictini (11) and a distinction between the two is evident in the gross appearance of the sting itself. The sting in the Dorylini is widely spatulate whereas that of *Aenictus* is slender and more typical of a stinging ant.

In the New World dorylines (8), the only distinct difference in stings is between *Labidus* (13) and the other genera examined (12). This difference is based on the slightly different appearance of the anterior end of the sting bulb and may be a superficial difference since behavioral and chemical evidence supports a closer relationship between *Labidus* and some of the dorylines in the other group.

ABBREVIATIONS USED IN FIGURES

AA	Anal arc
AE	Anterior extension of sting bulb
A-L E	Anterolateral extension of sting bulb
AP	Anal pad
Br	Branches of free filaments
CD	Collecting duct
CG	Convuluted gland
DA	Dorsal apodeme of oblong plate
DG	Dufour's gland
FA	Fulcral arms
FF	Free filaments
Flx Pt	Point of flexion
Fu	Furcula
Go	Gonostylus

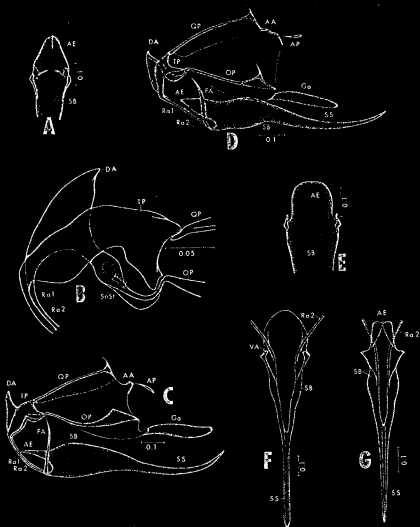


Fig. 7. — Sclerites of some New World Dorylinae. A — Anterior region of sting of *Eciton drepaniforme* F. Smith (DV). B — Triangular and oblong plates of *Eciton hamatum* (Fabricius) (ILV). C — *Eciton drepaniforme* (LV). D — *Eciton vagans* (Oliver) (LV). E — Anterior region of sting of *Eciton rapax* F. Smith (DV). F — Sting of *Eciton hamatum* (VV). G — Sting of *Nomamyrmex esenbecki* (Westwood) (DV).

Ln	Lanceet
MD	Main duct of poison sac
OP	Oblong
PS	Poison sac
QP	Quadrat plate
Ra 1	Ramus of first valvifer
Ra 2	Ramus of second valvifer
SB	Sting bulb
Se	Sensory setae
Sp	Spiracle
SP	Spiracular plate
SS	Sting shaft
St	Sting
TP	Triangular plate
Va	Valve
VA	Ventral apodeme of sting bulb
Muscles:	
3	Deflector of sting
4	Rotator or pivot of sting
II-VII	Second through seventh abdominal segments

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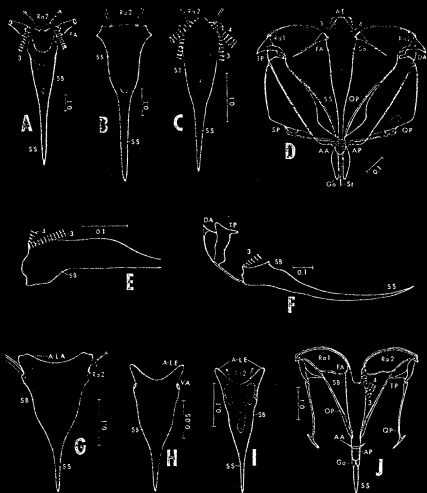


Fig. 8—Stings and some associated structures of some Ponerinae, Dorylinae and Cerapachyinae. A—Sting and associated muscles of a species of *Acanthostichus* Mayr (DV). B—Sting of *Phyracaces bicolor* Forel (DV). C—Sting and associated muscles of *Syscia typhla* Roger (DV). D—Poison sclerites of *Cheliomyrmex morosus* F. Smith (DV). E—Anterior end of sting of *Sphinctomyrmex steinhelli* Forel (LV). F—Sting and associated sclerites of a species of *Acanthostichus* (LV). G—Sting of a species of *Dorylus* (*Typhlopone*) Fabricius (DV). H—Sting of *Dorylus* (*Dorylus*) *braunsi* Emery (DV). I—Sting of *Dorylus* (*Anomma*) *molestus* (DV). J—Poison sclerites of *Aenictus gracilis* (F. Smith) (DV).

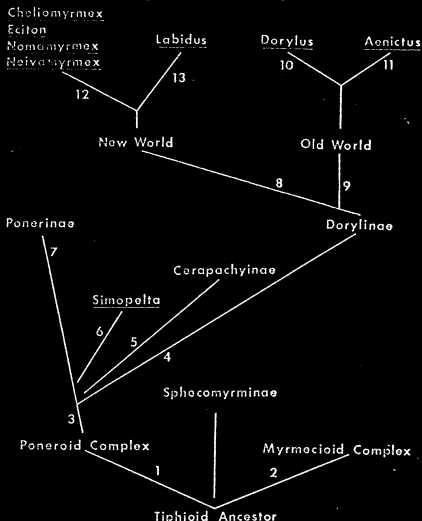


Fig. 9. — Possible evolution of some of the Ponerinae, Dorylinae and Cerapachyinae based on poison apparatus anatomy. Assuming a tiphoid ancestor, two major groups split off to form Poneroid (1) and Myrmecoid (2) Complexes. Fusion between furcula and sting bulb led to the Dorylinae (4) and Cerapachyinae (5). Near the doryline — ponerine branch, *Simopelta* (6) split from the main ponerine stock (7). The Dorylinae (4) later split into two distinct groups, the New World (8) and Old World (9) forms. Old World dorylines are represented by two forms, *Dorylus* (10) which has a definite spatulate sting and *Aenictus* (11) which has a sting most closely resembling that of a stinging species. New World dorylines split into two groups, one represented by genera having a well developed anterior sting bulb extension (12) and the other having a truncate anterior end to the sting bulb (13).

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